

## Importance of vegetation structure to the assembly of an aerial web-building spider community in North American open grassland

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**Abstract.** Spatial and temporal heterogeneity of suitable habitat in grasslands can promote species and functional diversity in arthropods, including responses by ubiquitous web-building spiders. A field experiment in tallgrass prairie habitat was performed to examine the response in abundance and web-type richness of aerial web-building spiders to changes in the availability of structure for web placement (vegetation architecture). To test the hypothesis that vegetation structure contributes directly to the web-builder abundance and web-type richness in open grasslands, we increased vegetation structure by adding dead woody stems of a common shrub along transects in each of three watersheds that differed in burn histories and existing habitat structure. Aerial web-building spiders were visually censused before and after the manipulations, at which time we recorded web-orientation, height, web-type, and the presence/absence of the spider associated with a web. Over the duration of the study, a total of seven web-type groups were encountered, of which medium-sized orb weavers were the most abundant web-building group across all watersheds. In general, higher spider abundances of orb-building spiders were observed in sections with added structure compared to the non-manipulated sections. However, reduced richness of web types was found on the manipulated sections of transects, suggesting that the architecture provided by woody stems does not provide sufficient and appropriate web-anchoring structure for the full range of web-building spiders groups in tallgrass prairie.

**Keywords:** Web types, heterogeneity–biodiversity hypothesis, habitat structure, Konza, tallgrass prairie

Spiders are ubiquitous, generalist and functionally important arthropod predators in terrestrial ecosystems, including grasslands, where they can reach high levels of local species richness and abundance (Diehl et al. 2013; Malumbres-Olarte et al. 2013). In grasslands, interactions among fire, ungulate grazing, plant species diversity, and climate are key drivers determining habitat structure. In turn, consumers respond to bottom-up processes that promote significant spatial and temporal heterogeneity of habitat structure (Bonte et al. 2000; Fuhlendorf & Engle 2001, 2004; Joern 2005). An overarching hypothesis here is that the overall abundance and species diversity of consumer communities increases with increasing spatial heterogeneity of critical habitat attributes, including the overall variability in vegetation architecture and plant species diversity (Dennis et al. 1998; Fuhlendorf & Engle 2001; Fuhlendorf et al. 2006; Jimenez-Valverde & Lobo 2007; Allouche et al. 2012).

Habitat structure affects species interactions in spider communities in multiple ways (Jones & Syme 1998). More precisely, vegetation complexity has been recognized as an important factor influencing species presence, richness and composition of spider communities (Jimenez-Valverde & Lobo 2007). Spiders can partition habitat at fine scales, facilitating the presence of different hunting strategies, where different prey species are susceptible to different hunting strategies (Schmitz & Suttle 2001; Wise 2006; Malumbres-Olarte et al. 2013). Microhabitat partitioning has been documented in web-building spiders where webs differ in placement height, orientation, or type depending on vegetation structure (Enders 1974; Brown 1981; Schmitz & Suttle 2001; Wise 2006). Structural complexity of the habitat can also lead to reduced spider mortality by providing refuges from predation or by influencing intraguild interactions (Finke & Denno 2002; Malumbres-Olarte et al. 2013). Thus, understanding habitat characteristics that affect web placement can reveal whether and how the structural complexity of the habitat can modulate spider community assembly,

species abundance and overall functional diversity (Robinson 1981; Bultman & Uetz 1982; Jimenez-Valverde & Lobo 2007; Diehl et al. 2013). In this sense, non-trophic effects on spider communities associated with habitat heterogeneity in plant architecture act as a “bottom-up template” for structuring spider assemblages (Halaj et al. 2000).

Open grasslands are dominated by non-woody vegetation, where graminoids comprise about 80% of the above ground vegetation biomass, while forbs often comprise about 80% of the plant species diversity (Knapp & Seastedt 1998; Joern & Laws 2013). Variation in vegetation architecture among habitats could result in different spider assemblages across the landscape. Web builders are a diverse group of predators representing ~ 60% of the North American spider fauna (Young & Edwards 1990), and web builders in US agricultural fields accounted for ~ 44% of the arachnid species richness associated to these ecosystems. These web-building spiders are mainly represented by the families Tetragnathidae, Araneidae, Linyphiidae, Theridiidae, and Dictynidae (Nyffeler & Sunderland 2003). However, web-building spider guilds are uncommon in North American open grasslands, seemingly because of a paucity of structure on which to anchor webs (Baldissera et al. 2004; Podgajski et al. 2013). Grassland ecotones with woody vegetation along waterways or woodlots often exhibit sharp boundaries characterized by rapid changes in habitat structural complexity, vegetation height, and dominant plant cover. The functional composition of spider communities also changes routinely along this structural gradient, where guilds of web builders are common at the woody end of the gradient but nearly absent in open grasslands (Baldissera et al. 2004).

We experimentally added woody structure in open grassland habitat to examine how changes in structural complexity affected aerial-web-builder abundance and the richness of web types. Our primary hypothesis states that the availability of structure for web placement limits density, richness of both



species and web types, and the distribution of web-building spider guilds in open grassland. We focused first on how web density and web-type richness responded to the newly added structures for web anchoring (woody vegetation: manipulation) in open grasslands. Second, we asked how increasing the distance at which structures for web anchoring are available relative to riparian woodland edges affects web density and web-type richness. If the availability of structures for web placements limits web-building spiders in open grassland, we predicted: (a) a greater density of web-building spiders and web-type richness will be found in areas with increased diversity and availability of web-anchoring structure, regardless of burn history at a local scale (300 m<sup>2</sup> transects) and distance from grassland-woodland edge; (b) the density of web-building spiders will be higher in watersheds with a history of lower burn frequency because the availability of structures for web placement increase with increasing time since the last burn; c) the distance from a riparian wood stand edge is expected to negatively influence the abundances or web densities of web-building spiders along transects to which we added structure for web placement; and (d) aerial web-builder abundances within manipulated sections will be higher than those in non-manipulated sections of these transects regardless of distance from edge. Web-type richness will be affected primarily by the availability of web-anchoring structures with lower richness on non-manipulated sections of the open grassland.

## METHODS

**Study site.**—This study was conducted at the Konza Prairie Biological Station (KPBS) located in the Flint Hills grassland of north-eastern Kansas, 10 km south of Manhattan (39° 05' N, 96° 35' W). KPBS is a 3487 ha native tallgrass prairie preserve that experiences a highly variable US continental climate consisting of wet, hot summers and dry, cold winters (Knapp & Seastedt 1998; Joern 2005). KPBS is a protected research area with long-term, landscape-level treatments that manipulate prescribed fire (1, 2, 4 and 20 year frequencies) and large ungulate grazing. Mean annual precipitation is 835 mm, most of which falls during the growing season. Steep-sloped terrain overlain by shallow soils and limestone benches unsuitable for cultivation characterize the topography of the site. The KPBS flora includes a mixture of more than 600 species (Towne 2002), including warm-season and cool-season grasses, legumes, and other forbs. The vegetation cover of KPBS is dominated predominately by perennial warm-season C<sub>4</sub> grasses although forb species contribute more than 80% of the plant diversity (Towne 2002). Prescribed burns in the watershed used in this study were initiated in 1972 (Knapp & Seastedt 1998; Collins & Calabrese 2012). Vegetation structure and species diversity has diverged over time, resulting in watersheds that vary from largely open grassland habitat with little woody cover to those with extensive invasion from woody vegetation in watersheds subjected to low fire frequency treatments (Briggs et al. 2002; Ratajczak et al. 2012) and along the riparian areas (Knight et al. 1994; Collins & Calabrese 2012). Woody plant encroachment is characterized by increased woody and forb cover at the expense of grass cover (Wilcox & Huang 2010), providing an ideal structurally complex and spatially heterogeneous habitat for web-building spiders.

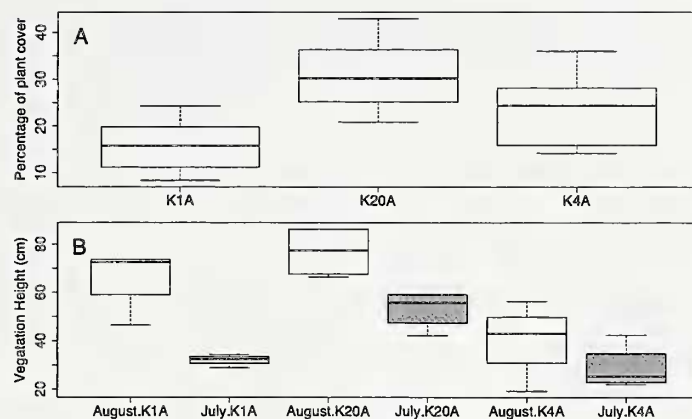


Figure 1.—(A) Comparison of the percent cover of plants with complex architecture (forbs and woody vegetation) among watersheds at Kings Creek basin. (B) Comparison of the vegetation height of the grass layers between early July (shaded) and mid-August (open). The box plot elements represent the following: box vertical dimension = interquartile range; horizontal line = median; whiskers = the minimum and maximum values.

Our study was conducted on three ungrazed watersheds (K1A, 113.9 ha; K4A, 53.16 ha; K20A, 83.13 ha) with fire frequency histories of 1, 4 and 20 years fire return intervals, respectively. All three watersheds were burned in spring 2013 just weeks prior to commencing this experiment, resulting in similar understory vegetation layers in all three watersheds. However, woody plant and forbs vegetation cover still differed among watersheds (ANOVA,  $F_{2,18} = 25.3$ ,  $P < 0.0001$ ; Fig. 1A). Vegetation height differed among watersheds (ANOVA,  $F_{2,18} = 16.2$ ,  $P < 0.0001$ ) and among the early (June) and late (August) part of the growing season (ANOVA,  $F_{2,18} = 28.1$ ,  $P < 0.0001$ ; Fig. 1B), reflecting the legacies of burn history. Vegetation in these watersheds ranged from an open grass canopy in K1A with little woody vegetation to abundant woody shrub islands (a mixture of *Prunus* species, *Cornus drummondii*, and other shrub species) in watershed K20A; watershed K4A was intermediate in woody structure and consists primarily of open grass canopy with incursions of shrub islands.

**Study design.**—To test the hypothesis that available structure for web placement limited the abundance and richness of web types in open grassland, woody structure was added along sections of the transects. In each of the three watersheds (K1A, K4A and K20A), we established four transects (100 m long by 3 m wide) beginning at the transition edge between a riparian woody stand near King's Creek and open grassland. We placed one end of all transects at the edge of woody riparian vegetation because we expected this transition zone to serve as a source of web-building spiders for recruitment into open grasslands if a response occurred. This scheme also allowed us to determine whether distance from the edge of a woody stand affected aerial-web-builder recruitment into open grasslands when woody structure is added at different distances from this transition zone.

We manipulated habitat structure by adding woody stems of *Cornus* (dogwood) (experimental treatment) to randomly selected, 25 m sections for each 100 m long transect during July 1–4. The rest of each transect (75 m) served as a control. Two aluminum wires were stretched along five, evenly

Table 1.—Web-building spider functional groups at KPBS and diversity associated with each functional group. Sample specimens were collected on August 2013 and identified to genus with the exception of the Dictynidae, which were no longer active in the field at this time of the year.

Web morphology	Family	Genus	Web size (cm <sup>2</sup> )	
			Min.	Max.
Small-orb	Araneidae	<i>Micrathena</i>	4	< 50
Medium-orb	Tetragnathidae Araneidae	<i>Tetragnatha Acanthepeira, Argiope, Cyclosa, Larinioides, Mangora</i>	> 50	740
Large-orb	Araneidae	<i>Neoscona</i>	> 740	3239
Funnel-web	Agelenidae	<i>Agelenopsis</i>	9.43	2842
Doily-sheet-web	Linyphiidae	<i>Frontinella</i>	5	506
Irregular-all-direction-web	Theridiidae	<i>Euryopis, Theridion</i>	55	566
Irregular-mesh-web	Dictynidae		4	12

distributed fence posts (top and bottom) along the 25 m spans to serve as support structure for the dead *Cornus* stems. Stems that ranged in height between 1.5–2 m were collected nearby. To obtain a canopy diameter of approximately 60 cm, groups of two to three stems were tied to the wires approximately every 2.5 meters. Upon installation, the *Cornus* stems were immediately and carefully examined for the presence of spiders; none were detected during this installation phase. Transects were left unchecked for eight days to allow naturally dispersing spiders to colonize the structures before the first of three post manipulation censuses was conducted in the second week of July.

**Sampling the spider community.**—Web builders are a diverse group of predators representing ~ 60% of the North American spider fauna (Young & Edwards 1990). They are uncommon in North American open grasslands relative to other spider groups, seemingly because of a paucity of structure on which to anchor webs (Baldissera et al. 2004; Podgaiski et al. 2013). Aerial web-building spiders were visually censused up to 1.5 m away on each side of the 100 m long transects; each transect was spaced 50 meters from the neighboring transects and censused five times during a three month period – two times in June before the habitat structure manipulation, and three times after the addition of woody structure (second and fourth week of July and third week of August). Visual censuses are effective for counting spiders with conspicuous webs, and spiders remain undisturbed in the study area and can be found repeatedly throughout the study period (Lubin 1978). Reference samples for each species were taken during our last survey in August to identify families and species, and to define their respective web types. For each web, we recorded the orientation (vertical, diagonal, horizontal or no clear orientation), height above the ground, web type (orb, bowl, sheet, funnel, threads without a clear structure), two measurements of web diameter to estimate area for prey capture in the web, and the presence or absence of the spider.

In the field, we used web structure to identify webs to family if spiders were not present on the web (Halaj et al. 1998; Uetz et al. 1999; Eisman et al. 2010). Family identity was confirmed on site for webs with resident spiders. Irregular, hackled silk around the heads of flowers, branches and dead stalks were classified as Dictynidae and sheet webs as Linyphiidae. Even though Linyphiidae is a very diverse family of sheet web builders in the US, representatives of this family tend to be less common (usually < 25% of total spider individuals)

(Nyffeler & Sunderland 2003). Because we sampled only aerial webs in this study while most linyphiids build their webs near the ground, we only found individuals of the genus *Frontinella* F.O. Pickard-Cambridge, 1902 as representatives of this family. Thus, the linyphiids are likely underrepresented in our surveys. All funnel webs were considered Agelenidae, and irregular cobwebs were classified as members of Theridiidae. Vertical and diagonally oriented orb webs were classified as Araneidae if the web had a closed center hub while webs with an open center hub were designated as Tetragnathidae.

We measured 740 webs from six families and 12 genera over a three-month period. Following Uetz et al. (1999) and Eisman et al. (2010), we divided the web-builder spider community into five web-type groups: Orb web builders, Funnel web builders, Doily-sheet web builders, Irregular-all-directions web builders and Irregular-mesh web builders. Because of the large variation in orb-web diameters, we further divided this web-type group into three size classes, small (< 50 cm<sup>2</sup>), medium (> 50–740 cm<sup>2</sup>), and large (> 740 cm<sup>2</sup>), using as a reference a subset of data from those orb-weaving spiders that were consistently identified to genus, species or morpho-species (Table 1).

**Habitat structure.**—Vegetation along the transects was measured twice during this study, once in early July before manipulating habitat structure and once in late August during the last spider survey. Habitat structural complexity (canopy structure: vegetation median height, mean height and number of vegetation layers) was measured using a modified point sampling technique (Joern 1979). A modified Robel pole was constructed using a 1.85 m copper tube (diameter 1.25 cm) demarcated with a scale of 5 cm increments. Canopy structure (habitat structural complexity) along transects was measured by taking measurements every 5 m along these transects (21 points per transect). At each point, the pole was placed within the vegetation perpendicular to the ground and the number of vegetation hits touching the pole in each 5 cm segment was recorded. “Vegetation median height” per transect was estimated as the average of the median for 21 sampling points along each transect. The “number of vegetation layers” at each site was based on vegetation touches in each 5 cm increment interval on the Robel pole. Values for the number of vegetation layers ranged from 1 to 37 layers per site, and at least two hits in a layer were required for a height interval to be considered a layer. “Vegetation cover composition” was estimated using a 0.1 m<sup>2</sup> quadrat, where cover was classified as open soil, litter, grass, forbs, or woody



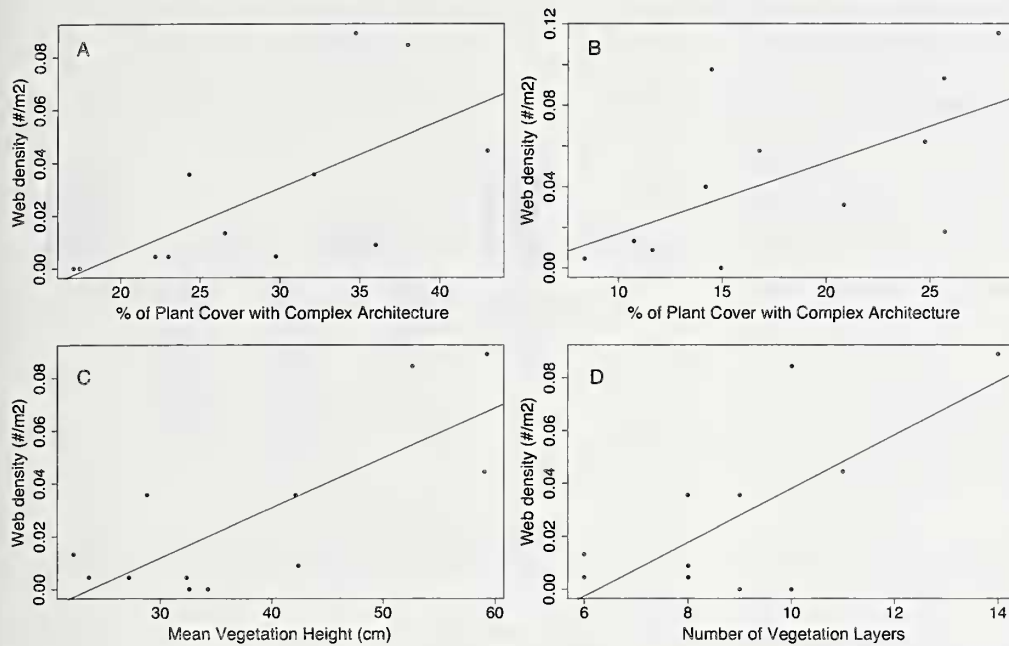


Figure 2.—Relationships between web density and percent plant cover in July (A) and in August (B). Relationships between web density and mean vegetation height (C) or number of vegetation layers (D) in July.

plant. Following the Daubenmire cover class method, the percentage of each vegetation cover class was scored as: 0 = 0%, 1 = 1–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 75–95%, 6 = 96–100% within each quadrat. Vegetation structure was scored three times in each 5-meter transect segment for a total of 60 estimates for each transect during each of the two vegetation sampling periods. Midpoints of cover classes were used in quantitative comparisons of samples and subsequent analyses (Daubenmire 1959). Because we were interested in how aerial-web-building spider abundance and the richness of web types responded to the availability of vegetation with complex architecture, we combined the values of forb and woody vegetation to obtain a better estimate of cover of plants with complex architecture.

**Statistical analyses.**—Because watersheds differed in the percentage cover of plants with complex architecture and complexity of habitat structure, linear regression analyses were performed separately for July and August to assess whether web density increased as habitat complexity increased from open grassland to habitats with extensive invasion from woody vegetation in the non-manipulated sections of the transects. For these analyses, we used vegetation surveys from July and August, the first of the two July spider surveys, and the August spider survey. We only used the web density values from the non-manipulated sections of these transects to avoid web-density bias effects driven by the addition of woody vegetation in the manipulated sections of these transects. Predictor variables to assess web density responses were: percentage of plants with complex architecture, Robel median, vegetation height, and number of vegetation layers.

We performed a 3-way analysis of variance (ANOVA) with repeated measures to determine the effects of adding habitat structure to aerial-web-builder density and richness of web types with respect to distance from riparian woodland edge. The response variables measured were: web density and richness of web types. We also explored the individual responses of the small-orb weaver and medium-orb weaver groups

to our habitat manipulation as these were the numerically dominant groups in our samples and commonly found in the experimental structures. The predictor variables were: stem manipulation (addition of woody vegetation vs. control), distance of 25 m experimental sections of these transects from the woodland edge (four levels: 0, 25, 50, 75 m) and survey (1–5) corrected for repeated measures per transects. Transects were treated as independent experimental units and the location of manipulated sections (0–25, 25–50, 50–75, 75–100 m) along transects were assigned randomly. Spider density and richness were calculated for each 25 m section of these transects for each survey period. Statistical analyses were performed using R 3.1.2 (R Core Team 2013) package *vegan* (Oksanen et al. 2011).

## RESULTS

**Spider responses to gradients in vegetation structure.**—Web density was positively related to an increase in percentage cover of plants with complex architecture, forbs and woody vegetation, both in July and August (Linear regression,  $F_{1,10} = 7.82$ ,  $R^2 = 0.38$ ,  $P = 0.02$ ;  $F_{1,10} = 5.53$ ,  $R^2 = 0.29$ ,  $P = 0.04$ , respectively; Fig. 2A, B). The density of aerial web builders increased with increased vegetation height (Linear regression,  $F_{1,10} = 15.51$ ,  $R^2 = 0.57$ ,  $P = 0.003$ ; Fig. 2C), and with an increase in the number of vegetation layers (Linear regression,  $F_{1,10} = 9.76$ ,  $R^2 = 0.44$ ,  $P < 0.01$ ; Fig. 2D) in early July. But these relationships were not significant in the late August survey (Linear regression,  $F_{1,10} = 0.5$ ,  $R^2 = 0.05$ ,  $P = 0.49$ ;  $F_{1,10} = 2.72$ ,  $R^2 = 0.14$ ,  $P = 0.13$ , respectively). These predictor variables suggest that web-builder density increased along a gradient of habitat structural complexity and web-anchoring availability driven by forbs and woody vegetation. No significant response was seen between web density and vegetation median height in either July or August surveys (Linear regression,  $F_{1,10} = 1.71$ ,  $R^2 = 0.06$ ,  $P = 0.22$ ;  $F_{1,10} = 0.67$ ,  $R^2 = 0.06$ ,  $P = 0.43$ , respectively). Results are consistent with the hypothesis that a greater abundance of aerial web-building spiders is found in areas with greater availability

of web-anchoring structure associated with increased structural complexity.

The richness of web types varied among the watersheds with K20A showing the greatest response in abundance and richness of web-anchoring structures. For example, Funnel-web-builder groups were more abundant than expected because of the abundance of web-anchoring structure close to the ground (dead woody stems), which was lacking in the other two watersheds. Due to the woody vegetation type selected for the manipulation, we did not influence the abundance and/or distribution of this group. Our results also showed that the Irregular-mesh-web builders (Dictynidae) were only present during the early part of this study, disappearing in late June (Supplemental material 1: online at <http://dx.doi.org/10.1636/P14-58.s1>), just prior to habitat manipulation. Thus, our habitat manipulation potentially influenced density and distribution of five out of seven web types groups of web-building spider found at KPBS.

**Web-building spider responses to increases in availability of web anchors in open grasslands.**—In general, we found that web density was higher on the manipulated sections of the transects. We found that distance from riparian-woodland edge affected aerial-web-builder density, where web density decreased with increased distance from woodland edge (ANOVA,  $F_{1,219} = 5.3$ ,  $P = 0.02$ ). Even though the manipulated section of these transects generally had higher web density, we found a strong interaction for manipulation-by-distance from the woodland edge (ANOVA,  $F_{1,219} = 4.0$ ,  $P = 0.048$ ; Fig. 3C). Web density in the manipulated sections decreased as the distance from the riparian-woodland edge increased, even though they still showed higher web densities than those seen in the non-manipulated sections of the transects. Results indicate that woody vegetation is a limiting resource for aerial web-building spiders in open grasslands systems. Of the five groups of web builders, only the density of the small-orb and medium-orb weaver groups (Fig. 3A, B) responded positively to the addition of woody web-anchoring structure (*Cornus* stems) in open grasslands (ANOVA,  $F_{1,221} = 8.0$ ,  $P = 0.005$ ;  $F_{1,221} = 6.0$ ,  $P = 0.015$ , respectively) regardless of distance from woodland edge or sampling period after manipulation.

To determine whether aerial web-building spider density responded quickly to structure availability, we compared densities from our second pre-manipulation (late June) survey to our first survey after manipulation (early July), which was conducted eight days later. Habitat manipulation led to a quick positive effect on small-orb weaver density (ANOVA,  $F_{1,77} = 5.2$ ,  $P = 0.026$ ); higher densities of this spider were observed in manipulated sections of transects when compared to non-manipulated sections, regardless of distance from wood stand edge.

Results showed differences in web-type richness among manipulated and non-manipulated sections of these transects (ANOVA,  $F_{1,221} = 5.5$ ,  $P = 0.02$ ). Web-type richness increased in the manipulated sections of these transects as the growing season progressed (ANOVA,  $F_{1,221} = 5.4$ ,  $P = 0.02$ ; Fig. 4) compared to the non-manipulated sections.

## DISCUSSION

The habitat heterogeneity hypothesis posits that the abundance and diversity of arthropod species will respond positively

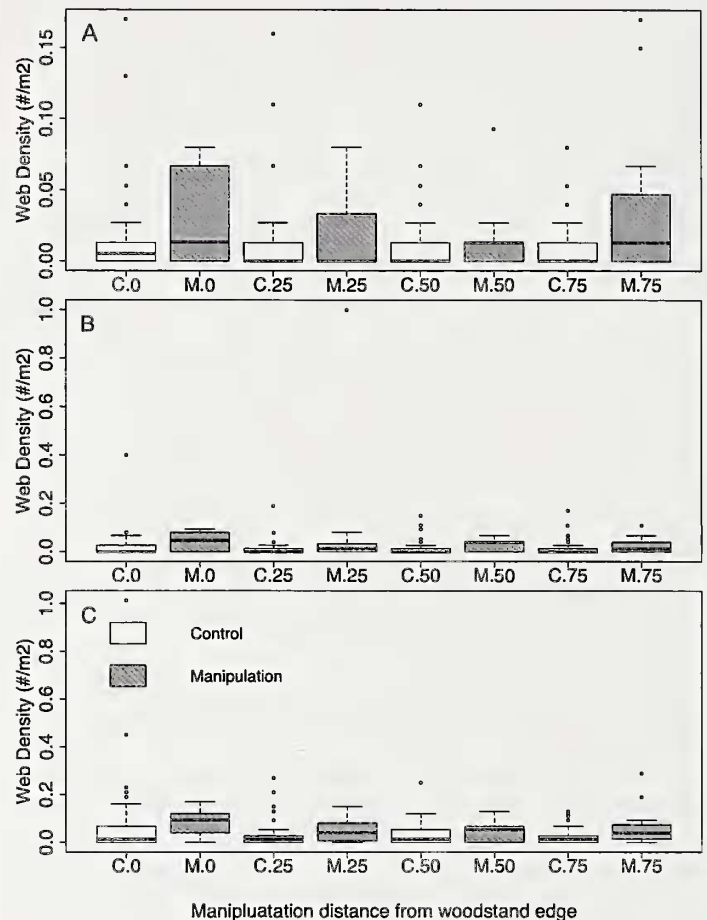


Figure 3.—Comparison of open grassland web-builder spider density among various distances from a riparian woodland edge at Konza Prairie Biological Station, Kansas. (A) Small-orb weavers, (B) medium-orb weavers, (C) total web density (all web types groups combined). The box plot elements represent the following: box vertical dimension = interquartile range; horizontal line = median; whiskers = minimum and maximum values; circular points = maximum observations 1.5(IQR) above the 75th percentile.

to increases in the spatial heterogeneity of plant species richness and vegetation architecture (Dennis et al. 1998; Fuhlendorf & Engle 2001; Fuhlendorf et al. 2006; Jimenez-Valverde & Lobo 2007; Allouche et al. 2012). It is well recognized that fire-grazing interactions in grasslands modulate habitat heterogeneity with great effects on the abundances, diversity and trophic complexity of consumer assemblages through bottom-up regulation mediated by plants (Joern 2005; Joern & Laws 2013). Thus, habitat structural complexity and local plant architecture diversity in particular are important factors influencing terrestrial arthropod diversity (Dennis et al. 1998; Halaj et al. 2000; Joern 2005; Cobbold & MacMahon 2012; Joern & Laws 2013), abundance, and community dynamics at multiple levels (Langellotto & Denno 2004). For example, intensive grazing by sheep in Hungarian grassland led to the loss of spider species sensitive to habitat disturbance and increased the representation of common and disturbance-tolerant species (Szinetár & Samu 2012).

In this study, we experimentally tested the proposition that availability of physical structure for web placement can limit aerial web-building spider communities in open grassland. We



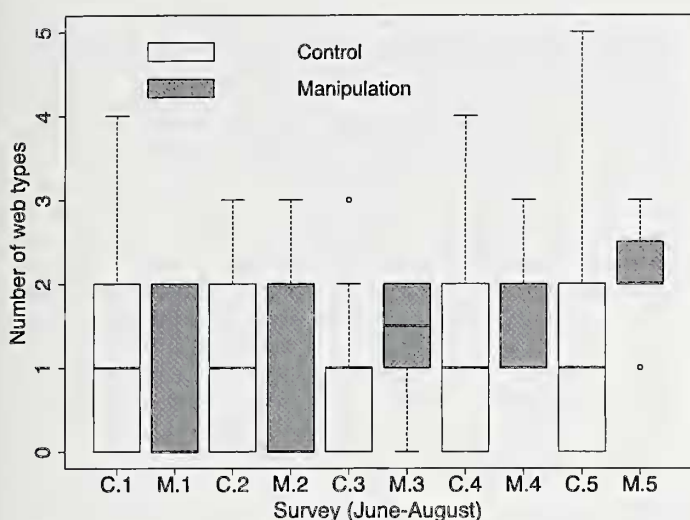


Figure 4.—Comparison of richness of web types among various distances from riparian woodland edge. The box plot elements represent the following: box vertical dimension = interquartile range; horizontal line = median; whiskers = minimum and maximum values; circular points = maximum observations 1.5(IQR) above the 75th percentile.

did so by increasing woody structure in the herbaceous-shrub layer at various distances from riparian woodland edge in three watersheds. Distributions of web-building spiders are directly linked to the spatial configuration of woody vegetation in their habitat due to web-anchoring requirements; both experimental and observational studies indicate the tight relationship between spider abundance and habitat structure (Halaj et al. 1998; Rypstra et al. 1999; Diehl et al. 2013). Vegetation examined among the three watersheds in this study ranged from an open grass canopy with little woody vegetation to watersheds with significant levels of woody vegetation encroachment and thus a significant gradient of habitat complexity. Indeed, our results for both July and August show that web-builder density increased as the percentage cover of forbs and woody vegetation increased from open grassland to grassland encroached by woody vegetation. In July, web-builder density increased with increasing number of vegetation layers as vegetation height increased, thus increasing the possibility of habitat partitioning by web-building spiders. The highest web densities along this habitat structure gradient were observed on watershed K20A, a watershed with a history of low burn frequency and a high accumulation of woody vegetation.

Several lines of evidence from our experiment suggest that the availability of web-anchoring structure limits web-building spiders in open tallgrass prairie. We found critical responses by aerial-web-building spiders to regions where web-anchoring structures were added. (a) There was a greater density of aerial-web-building spiders and richness of web types in manipulated areas at the transect scale (300 m<sup>2</sup> transect) towards the end of the growing season. (b) Web density on the manipulated section decreased with increasing distance from the riparian woodland edge, even though it was higher overall than in non-manipulated sections. (c) After *Cornus* stems were added, web-type richness increased over time until, by the end of the study, it was higher than in the control sections. Similar results were found by Toti et al. (2000), where species richness of aerial

web builders increased from spring to fall in grass habitat at the Great Smoky Mountains National Park. However, some transects in that study had control sections that consistently maintained high web types richness over the entire duration of the study, and the response was driven mostly by naturally high abundances and richness of web anchoring structures. (d) Finally, the addition of web-anchoring structure led to an increased density of small-orb and medium-orb web-builder groups in a watershed under frequent burn treatments, watersheds characterized by the paucity of woody vegetation cover. Even though small-orb and medium-orb densities were higher at the manipulated section than on the control sections at all distances from the riparian woodland edge as predicted, we also observed a decrease in the density of these two groups of web builders overall. Such results suggest that other factors such as species dispersal ability could affect their distribution on the habitat.

Web-building spider species differ in how webs are positioned within the vegetation, outcomes driven by differences in web type and web structure (e.g., spacing of mesh, web size, height of web placement, and the sizes of prey captured). Such variability in web placement constraints facilitates the assembly of web-builder diversity in habitats that are architecturally and floristically diverse (Richardson & Hanks 2009). Differences in the richness of web types seen among watersheds were associated with differences in habitat structural complexity and underlying variation in cover with complex architecture. Generally, we observed that web-type richness was higher in the manipulated sections of these transects even with exceptions from a few control sections from regions associated with dense, woody stands (e.g., *Cornus* shrub islands and/or diverse mixture of woody plant and forbs). Such sample sites with high overall structure could maintain high levels of web-type richness through the entire duration of the study. Such hotspots of web-type richness were found on all four transects of K20A watershed and one transect of K4A. We note that these hotspots not only supported diverse web-type richness but they also showed a higher diversity of web-building spiders species per web-type group than in samples from non-hotspot points along the same transect. Unfortunately, we could not directly analyze species richness in this study due to difficulty in identifying all species in the field and the lack of watershed replication in this study.

Habitat structure and vegetation architecture affect the spatial distribution of spiders with different web types (Colebourn 1974). For example, while our habitat manipulation using *Cornus* stems positively affected small-orb and medium-orb density at various distances from the riparian woodland edge, it did not influence the funnel-weavers, a common group of web builders at KPBS. The experimental design did not provide the appropriate web-anchoring structure close to the ground for assessing responses by funnel-weavers (Agelenidae) that were only found in open grasslands in zones with accumulation of woody stems near the ground in K20 and one transect in the K1A watershed. Even though, they were the most abundant web-building spiders found along the King's Creek basin in KPBS during the summer of 2012, Agelenidae densities dropped dramatically at the transition zone from riparian woodlands into open grassland (J.E. Gómez, unpublished data). Also, we could not address responses of the mesh-weaver group (Dictynidae) to increases



of web-anchoring structure in open grasslands as this group was only active early in the growing season and their abundance dropped by the end of June before our manipulation was conducted.

Even though vegetation structure is widely recognized as a key determinant resource of spider community composition, the exact mechanism for its influence is unknown and other indirect effects such as microclimate and prey availability may play important roles (Jimenez-Valverde & Lobo 2007). Initial colonization by spiders may be relatively quick because even large web spinners are capable of aerial dispersal at immature stages (Gibson et al. 1992). Our experiment demonstrates that spider density responded quickly to an increase in the availability of woody structure as new *Cornus* stems were colonized by multiple types of web-building spiders within a period of only eight days, and spider density was consistently higher on the manipulated sections when compared to the non-manipulated sections of these transects from mid- to late summer. We found that overall density responses of aerial-web builders to increased availability of web-anchoring structures were largely driven by the small-orb weavers and to a lesser extent by the medium-orb weavers. It makes sense that orb-weavers were the first colonizers (Blamires et al. 2007) as orb weavers occupy a wide range of habitats and accordingly there is a great diversity in both web architecture and behaviors among genera. For example, *Nephila* Leach, 1815 and *Tetragnatha* Latreille, 1804 build large webs in open habitats while *Argiope* Audouin, 1826 builds smaller webs among low, dense (closed) vegetation (Blamires et al. 2007). This increases the possibility that at least one species within an orb weaver web-type group could benefit from the architecture of *Cornus* stems. We conclude that the abundance and architecture of web anchoring structures limit aerial-web-builder density, distribution and richness of web type in the open grassland studied here.

Results from this study offer further support for the notion that structurally complex habitats provide a wider selection of web-attachment sites and thus increased habitat suitability for web-builder spiders in open grasslands in North America. Responses are facilitated by increased opportunities for spatial partitioning as the architectural complexity of the habitat increases (Robinson 1981), and responses likely operate at multiple scales.

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